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Vegetation of the Wet Windward Slope of Haleakala, Maui, Hawaii[1]

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ABSTRACT: The vegetation on the wet windward slope of Haleakala was studied for community organization along a transect between 350 m a.s.l. and the summit (3055 m). The plant communities classified by the Braun-Blanquet synthesis table technique showed a hierarchical arrangement and were correlated with altitude. First, the forest and the treeless vegetation were differentiated by two major species groups. The boundary between the two was coincident with the trade wind inversion (ca. 1900 m a.s.l.) where the wet, low to mid-altitudinal climate changed abruptly upslope to an arid high-altitude one. These two wide-ranging vegetation types were subdivided into three units, corresponding to three broad altitudinal zones: the lowland, the montane, and the high-altitude zones. The three units were further partitioned into seven plant communities, which indicated six altitudinal subzones and one dieback belt. The floristic composition of the communities, the community structures, and their environmental relationships are briefly described with a summarized differential table. The depauperate and disharmonic nature of the Hawaiian flora is reflected in such altitudinal patterns as the low species turnover and the depressed forest line.

THE HAWAIIAN ISLANDS, biogeographically the world's most isolated archipelago, support high endemism in their flora (956 flowering plant species with 89% endemic; Wagner et al. 1990). The extreme isolation has acted as a sieve allowing only a limited number of species to cross the ocean. As a result, the flora has become disharmonic (Hubbell 1968). For instance plants with larger disseminules are not common in the native inland forests in Hawaii. The flora is also depauperate, and the number of potential canopy species is low (Mueller-Dombois 1987).

The taxonomic disharmony and relative biotic impoverishment resulted in widespread monodominance of the native rainforests by *Metrosideros polymorpha* (Mueller-Dombois 1981*a*). This is a myrtaceous tree species with capsulate fruits, which produce very small wind-dispersed seeds. The species dominates the wetter Hawaiian habitats (Mueller-Dombois 1987).

The monodominance of *M. polymorpha* seems to be a factor in the recurring phenomenon of canopy dieback (Mueller-Dombois 1986, 1987). *Metrosideros polymorpha*, being shade-intolerant in the sapling stage (Burton and Mueller-Dombois 1984), depends on canopy openings to maintain its regeneration. Consequently, episodic stand-level regeneration in response to canopy dieback of *M. polymorpha* seems to have worked as a mechanism for successive generations. The process of dieback has been discussed as primarily a demographic phenomenon of cohort senescence, interacting with abiotic stresses (Mueller-Dombois 1988*a*).

We also suspect that the monodominance is manifested in reduced interspecific competition. Therefore, some distributional attributes of plant communities that are released from high species competition may be displayed on the slopes of the Hawaiian high mountains.

Investigations have been done to compare species turnover along mountain transects. One of the analyses relates to Haleakala,

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Maui, an isolated oceanic island mountain, the other to Mt. Kinabalu, Borneo, a species-rich continental island mountain.

In this paper, we present some results of the Haleakala transect study. The following questions guided this study: (1) Does a depauperate flora become organized into altitudinally definable communities? (2) If definable, are such altitudinal communities broader and fewer in number than in floristically richer areas? (3) How are the plant distribution patterns related to the altitudinal environmental gradient?

Study Area

The northeast slope of Haleakala (3055 m), Maui, exposed to the prevailing trade winds, was selected for the study. Haleakala is a shield-shaped volcano of early Pleistocene origin (0.8 million yr) and now quiescent. It is the third highest mountain in Hawaii (after Mauna Kea, 4205 m, and Mauna Loa, 4169 m). The summit, located at 20° 45′ N and 156° 15′ W, has a huge caldera (12 km long, 4 km wide) with cinder cones on its floor and exposed pyroclastic materials on the outer walls. The northeast slope is covered with soils derived from recent (late Pleistocene) volcanic rocks of the Kula volcanic series. There are also still younger (Holocene) rocks from the Hana volcanic series. The study area is located on the Kula volcanic series. The parent rock is largely from alkalic basalt (Stearns 1985).

The topography of the study area consists of undulating gentle slopes (generally less than 8°), dissected by numerous streams running parallel to one another downslope. The lateral dissections become steeper and wider near the coast, where they form deeply sliced, V-shaped valleys.

The study area is a belt transect, 1 km wide. It starts at 350 m a.s.l. near Kailua and extends upward on the interfluves of either side of Waikamoi Stream to the summit (Figure 1). The belt transect traverses three protected areas: a watershed forest (from 350 to 1600 m), managed by the East Maui Irrigation Company; the Waikamoi Preserve (from 1600 to 2100 m), managed by the Hawaii Nature Conservancy; and the summit area (from 2100 to 3055 m) in Haleakala National Park. Currently, the vegetation is relatively well protected. The summit area has been severely influenced by feral ungulates, particularly by goats (Stone 1985). But control efforts have supressed their activity. Feral pigs are the current major disturbance factor in the wetter forests (Stone 1985). The vegetation below 350 m a.s.l. has largely been converted to plantation forests.

Widespread forest dieback was noted in the lower segment of the transect and adjacent areas early in this century by Lyon (1909). Holt (1988) reassessed the same area. The vegetation of the summit crater was mapped by Whiteaker (1983).

Climate

There are great changes in climate over short distances along the transect, largely due to two factors: the altitudinal reduction of air temperature and the midslope increase in cloudiness. The climate of the windward lowland, classified as Af in Köppen's system (Köppen 1936), is warm-tropical and perhumid year-round. The summit climate, which may be classified as Cs in Köppen's system, is cool-tropical with a dry summer season.

The mean annual air temperature at the Kailua meteorological station (213 m a.s.l.), which is near the low end of the transect, is 21.5°C (Figure 2). The mean monthly temperature is 22.9°C in the warmest month (August) and 20.1°C in the coldest month (February). This indicates a maritime temperature regime, characterized by a small annual change (2.8°C). However, the diurnal fluctuation is nearly 10°C. Temperatures generally decrease upslope in accordance with the lapse rate of 0.55°C on Mauna Loa, Hawaii (Blumenstock 1961). However, Haleakala's upslope temperatures may divert from this lapse rate because of differences in cloudiness. Temperature increases sharply upslope at the trade wind inversion because of descending dry air. Results of a short-term measurement in June 1988 (Figure 2) indicate the presence of the

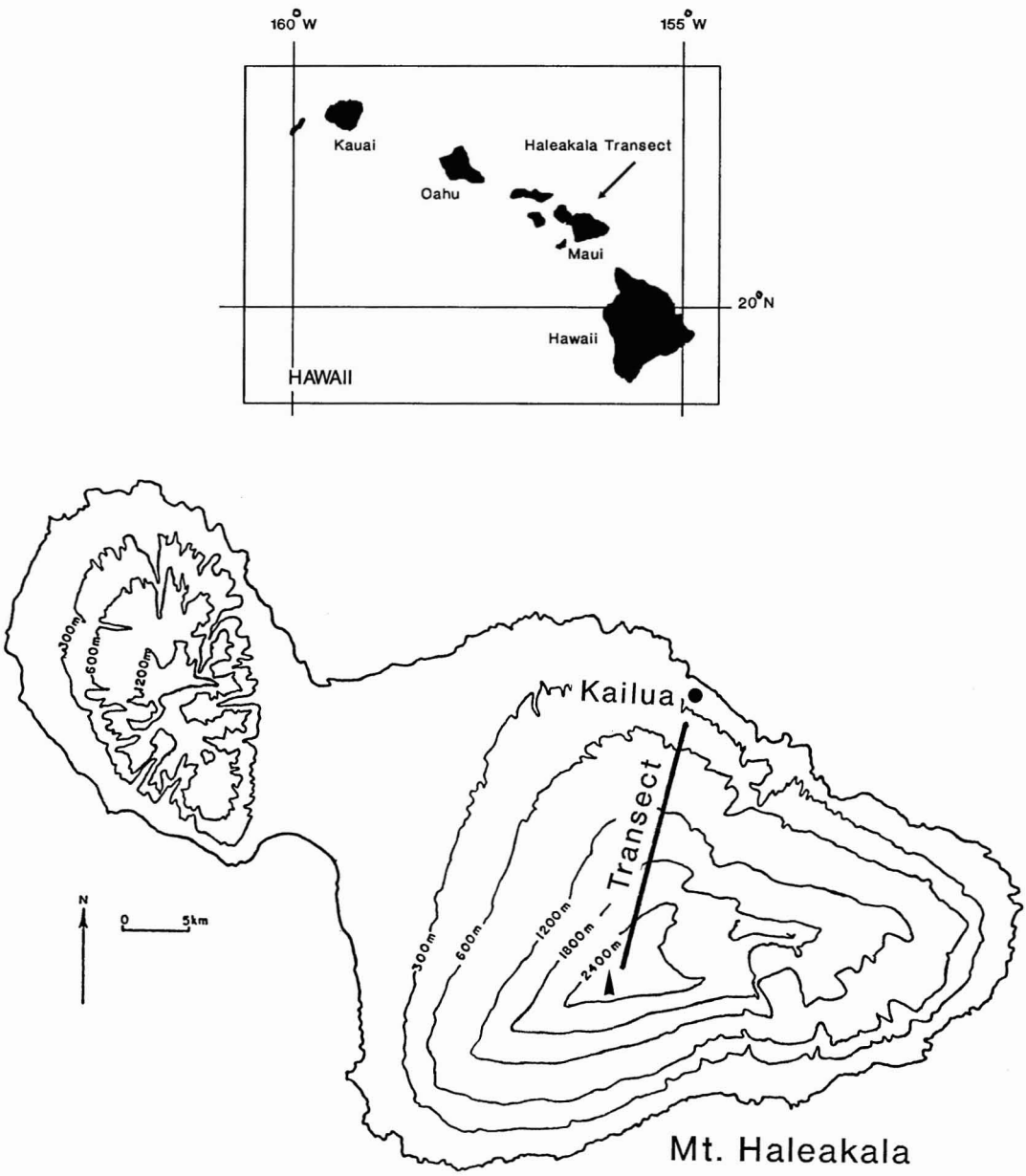

FIGURE 1. Location of the transect established on the windward slope of Haleakala, Maui, Hawaii.

inversion at 1900 m with a sharp temperature increase by 5°C. The inversion fluctuates, but most frequently appears between 1900 and 2000 m (Mendonca and Iwaoka 1969, Noguchi et al. 1987). At the summit (3055 m), the mean monthly air temperature is ca. 6°C in the coldest month, and slightly exceeds 10°C in the warmest month.

Noguchi et al. (1987) estimated the occurrence of ground frost to be 187 days per year

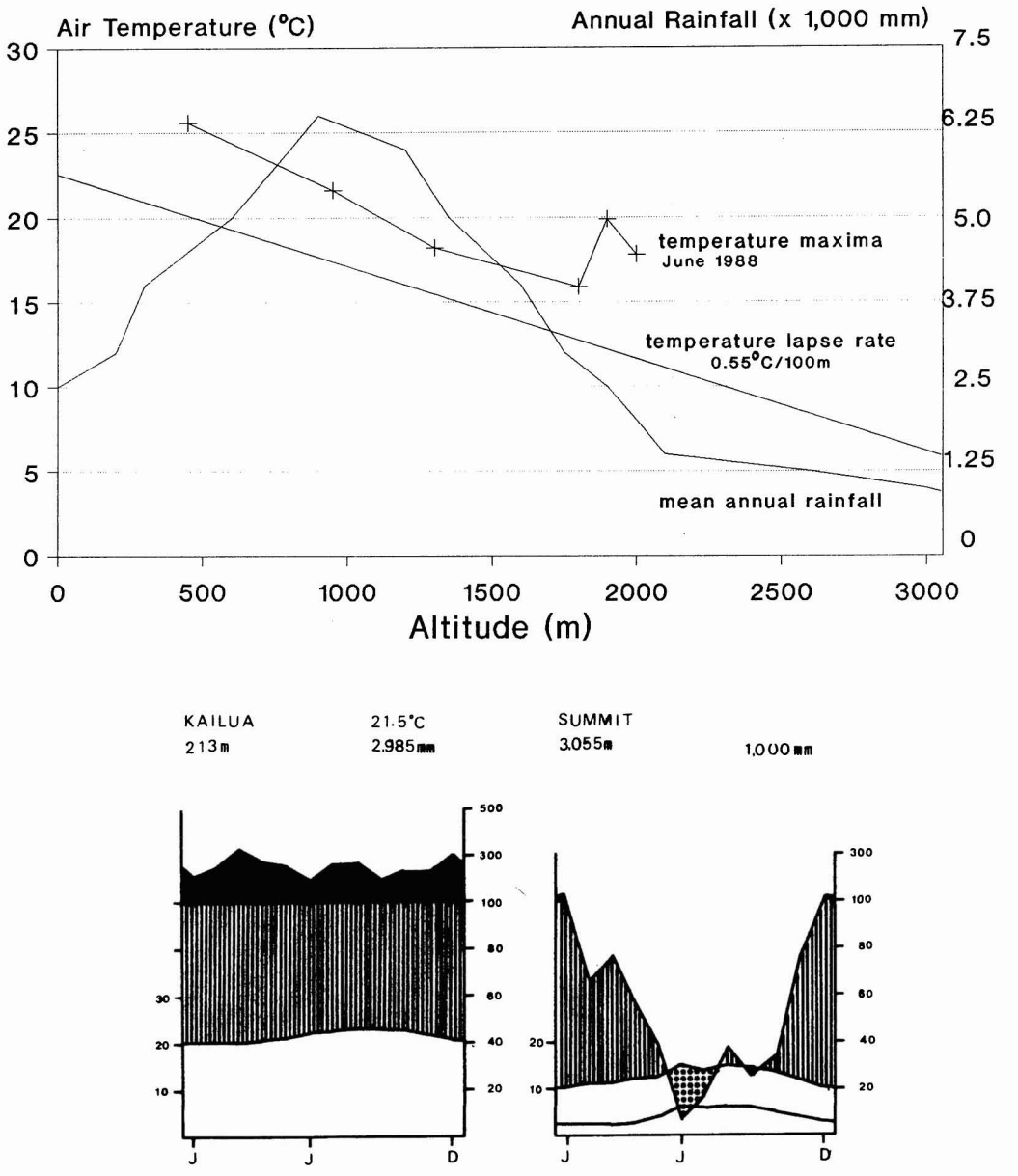

FIGURE 2. Climate along the transect. The climate diagram of Haleakala's summit is shown with monthly mean daily maximum and minimum air temperatures. The air-temperature lapse rate, 0.55°C/100 m, is a theoretical value. The air temperature maxima measured in June 1988 indicate an inversion at 1900 m.

at the summit. They also found evidence of ground frost as low as ca. 2700 m a.s.l. This elevation coincides closely with the ground-frost line of Mauna Loa found by Mueller-Dombois (1967).

The moisture regime of the northeast slope of Haleakala is largely controlled by the northeast trade winds and the trade wind inversion (Lyons 1979). The orographic uplift of the trade winds results in high rainfall

below the inversion. Rainfall rapidly increases upslope, from 4000 mm at 350 m a.s.l. to a maximum mean annual amount of 6500 mm at ca. 1000 m a.s.l. (Giambelluca et al. 1986; Figure 2). A dry area occurs above the inversion because clouds are prevented from moving upward by the inversion; the mean annual rainfall at 2000 m a.s.l. is 2000 mm and becomes less than 1000 mm at the summit (3055 m). In the midslope area, the total precipitation may far exceed the annual rainfall because of fog interception by the forest canopy (Juvik and Ekern 1978).

METHODS

The comparative transect method (van der Hammen et al. 1989) was employed to enable comparisons of the results of this study with those of other tropical high mountains.

The belt transect was stratified into even altitudinal intervals of 100 m to locate vegetation sample plots (i.e., relevés). In each interval, relevé analyses (Mueller-Dombois and Ellenberg 1974) were performed in several quadrats of 20 × 20 m by a system of stratified sampling: one relevé in the most developed stand of a gentle slope and several additional relevés under various canopy conditions ranging from widely opened to closed canopies. In these relevés, species composition, species cover using the Braun-Blanquet cover-abundance scale (Mueller-Dombois and Ellenberg 1974), layer structure, and physical environment were recorded. The quadrat size of 20 × 20 m, chosen for allowing direct comparisons to other Hawaiian rainforest studies done with the same quadrat size, exceeded the minimal area. Some low-growing stands were sampled with 10 × 10 m quadrats, which also satisfied the minimal area requirement. Nomenclature follows the Flora of Wagner et al. (1990) for flowering plants and an unpublished checklist (1987) of W. H. Wagner and F. S. Wagner for pteridophytes.

A soil profile was described from a representative stand in every 200-m altitudinal interval. Soil color, texture, mottling, root distribution, and other properties were noted for each horizon.

RESULTS

General Description of the Soils

The soils below the inversion are wet and histic. Gleyed B horizons (dark gray) due to anaerobic conditions with an overlay of thick mors (10–30 cm) are characteristic of such wet histic soils. The soils are highly acidic, with pH values between 3 and 4. They probably exhibit toxic levels of aluminum (unpublished data). Above the inversion, the soils are drier and better drained.

A strongly reduced subsurface horizon is found in the lowland, particularly on the flat interfluve between 450 and 600 m a.s.l. despite the fact that the midslope receives even higher rainfall. The reducing conditions are probably related to the almost flat or gently sloping topography, which prevents rainwater from draining laterally and aggravates the anaerobic condition. A still further degraded soil type with a placic horizon consisting of an iron hardpan beneath the B horizon is found in the lowest segment at 450 m a.s.l.

The montane soils have less strongly gleyed horizons and thicker peaty organic horizons than the lowland soils. Some soil profiles between 1000 and 1600 m a.s.l. show clearly eluviated horizons underneath the organic horizons, suggesting strong leaching with lower water tables whose levels may fluctuate only below the eluviated horizons. Concave to flat montane slopes are completely saturated.

The soils gradually become better drained toward the inversion, where thin gley horizons are still recognizable but waterlogging no longer appears.

The soils above the inversion are less developed, showing fewer horizons and diffuse boundaries. Associated with the lower rainfall and the better drainage, the soils are weak to neutral in acidity (pH 5–6) and high in cation contents (unpublished data). The soils in the subalpine zone have loamy textures and thicker A horizons (exceeding 50 cm). They resemble grassland soils.

The land above 2700 m is stony. The soils can be placed in the order of Entisols. They lack pedogenic horizons, and incorporated organic matter contents are low.

General Description of the Vegetation

Using a total of 111 relevés comprising 189 taxa, the vegetation along the transect was hierarchically classified by the Braun-Blanquet synthesis table technique (Mueller-Dombois and Ellenberg 1974). However, our aim was not the designation of abstract communities into a hierarchical ranking, but rather a local classification of communities along the transect. The vegetation types classified here have not yet been compared with other comparable vegetation. Therefore, the nomenclature for the diagnostic species in the following description does not refer to the traditional terms: groups of differential species may contain both character and differential species.

At the first level, two vegetation types, contrasting in physiognomy (forest vegetation versus treeless vegetation), are differentiated by mutually exclusive species. This results in two major differential species groups. At the second level, the forest vegetation is subdivided into two units, while the treeless vegetation remains one unit. At the third level, these three units are further partitioned into seven plant communities: one of these is split into two subunits, yielding a total of eight units (noda). The subunit is a floristic variation of a community and is diagnosed by a group of species that are absent only in other subunits of the same community. The classified plant communities are named by their leading species. They are shown in the summarized differential table (see Appendix).

The floristically classified vegetation units are well correlated with altitude (Figure 3). The three broader units are identified by three species groups: the *Elaphoglossum crassifolium* group, the *Vaccinium calycinum* group, and the *Dubautia menziesii* group. These correspond to three broad ecological zones, respectively the lowland, the montane, and the high-altitude zone. The seven plant communities in the lower hierarchy are defined by seven species groups with more restricted amplitudes, which indicate finer zonal arrangements of vegetation within the broader altitudinal zones.

Many alien species are sporadic in distribution and remain unclassified. However, several alien species appear preferentially in certain zones, have high constancy values, and are assembled in associations.

I. Forest Vegetation

Forest vegetation extends over the lower two-thirds (from 350 to 1950 m a.s.l.) of the slope. The forest line (1950 m a.s.l.) coincides with the level where the trade wind inversion appears most frequently.

Fourteen endemic taxa (*Metrosideros polymorpha* var. *glaberrima*, *Cheirodendron trigynum*, *Vaccinium dentatum*, *Myrsine lessertiana*, *Broussaisia arguta*, *Athyrium microphyllum*, *Astelia menziesiana*, *Carex alligata*, *Polypodium pellucidum*, *Hedyotis* (*Gouldia*) *terminalis*, *Athyrium sandwichianum*, *Sadleria pallida*, *Myrsine sandwicensis*, and *Smilax sandwicensis*), five indigenous species (*Elaphoglossum hirtum*, *Ilex anomala*, *Pleopeltis thunbergiana*, *Asplenium polyodon*, and *Asplenium lobulatum*), and one alien species (*Rubus argutus*) are associated with each other.

These species differentiate the forest vegetation from the treeless vegetation. They have extremely broad altitudinal distributions spanning either the entire or most of the forested zone. Of the 20 differential species, only *M. polymorpha* var. *glaberrima* (a glabrous-leaved variety of *M. polymorpha*), *I. anomala*, and *C. trigynum* are potential canopy trees, and the rest of the species are understory components. Therefore, in this forest vegetation even the undergrowth taxa in lower layers or those with lower cover values have broad altitudinal distributions.

The tree cover is monodominant in its entire range, dominated by a single species, *M. polymorpha*, in spite of various habitat types encountered within the forest range. *Cheirodendron trigynum* is persistent in the canopy but low in cover.

Trees of *Metrosideros* commonly, except at the upper limit of closed forest, show gnarled morphologies that may be indicative of oligotrophy (Grubb 1977). Most of the trees are perched on fallen logs or on mounds of peat underlain by waterlogged soils. Tree heights and diameters are reduced in relation to the severely anaerobic soils downslope. They show an unusual altitudinal pattern: trees are most stunted (merely 2 m tall) at 450 m a.s.l.

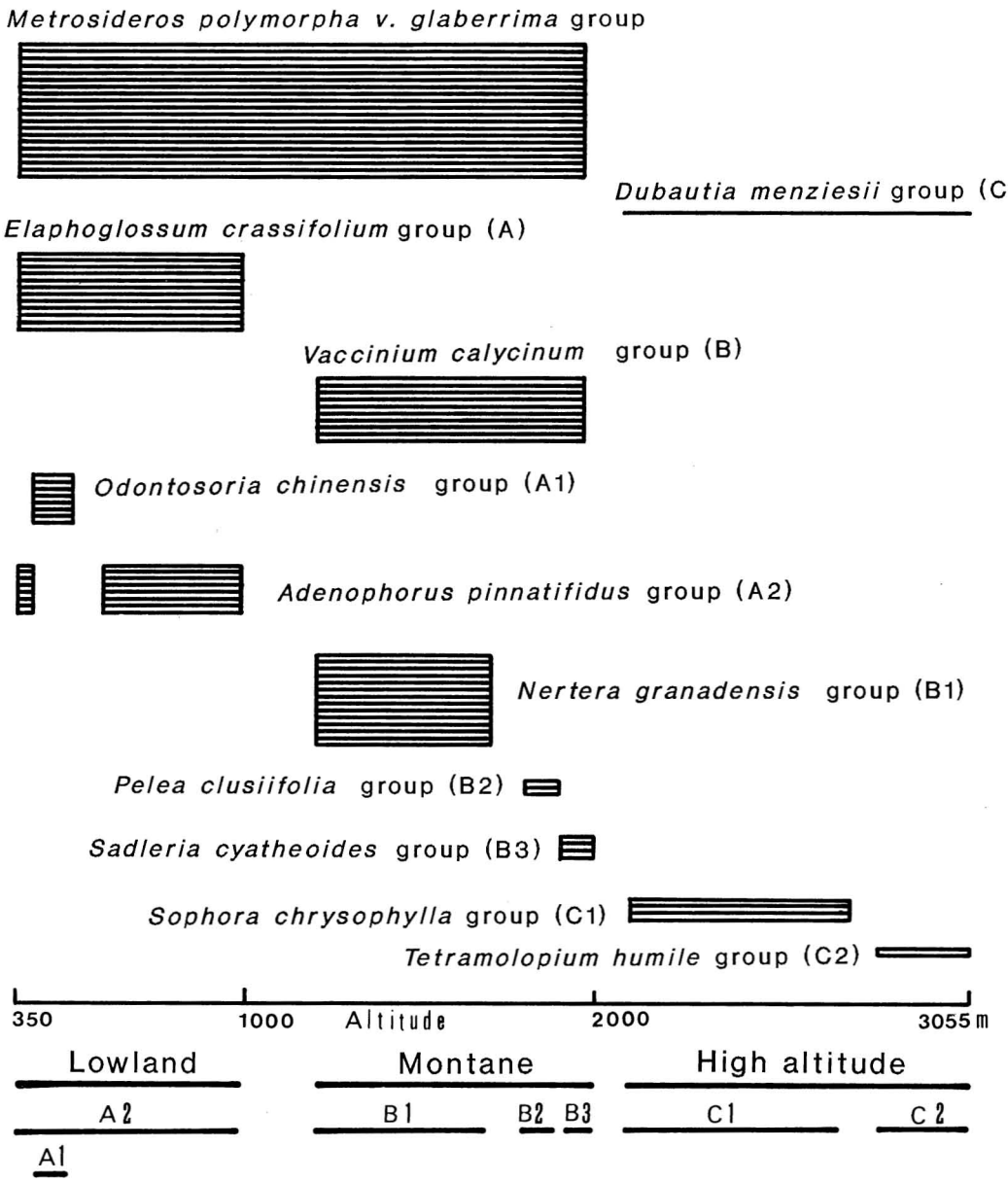

FIGURE 3. Altitudinal distributions of selected differential species along the transect.

They gradually increase in size upslope. The maximum bole height of 17 m and the maximum diameter of nearly 70 cm was found at 1800 m a.s.l., near the upper limit of the closed forest (1850 m). Above the closed forest limit, trees again decline in size. Saplings and seedlings of *Metrosideros* are common in canopy gaps, but they are scarce under closed canopies.

Effects of exotic plants are evident in the lower forest zone, as they are in other parts of Hawaii (Vitousek et al. 1987). The mid and upper segments are almost purely native.

The forest vegetation is floristically parti-

tioned into two units: A, *Elaphoglossum crassifolium* unit and B, *Vaccinium calycinum* unit.

A. *Elaphoglossum crassifolium* unit (lowland zone)

The *Elaphoglossum crassifolium* unit occurs below 1000 m a.s.l., corresponding to the lowland zone. Four endemic species (*E. crassifolium*, *Adenophorus hymenophylloides*, *Antidesma platyphyllum*, and *Tetraplasandra oahuensis*), four indigenous species (*Psilotum complanatum*, *P. nudum*, *Huperzia phyllanthum*, and *Nephrolepis cordifolia*), and four alien species (*Paspalum conjugatum*, *Cyperus halpan*, *Rubus rosifolius*, and *Setaria palmifolia*) are associated with each other and differentiate this unit.

The following two plant communities are distinguished in this unit: A1, *M. polymorpha* var. *glaberrima–Odontosoria* (*Sphenomeris*) *chinensis* community and A2, *M. polymorpha* var. *glaberrima–Adenophorus pinnatifidus* community.

A1. *M. polymorpha* var. *glaberrima–Odontosoria chinensis* community (lowland dieback belt, stunted open-canopy evergreen scrub) (see Figure 4*a*)

The *M. polymorpha* var. *glaberrima–Odontosoria chinensis* community, differentiated by two indigenous species (*O. chinensis* and *Machaerina mariscoides*) and six alien species (*Andropogon virginicus*, *Psidium cattleianum*, *Centella asiatica*, *Sacciolepis indica*, *Tibouchina herbacea*, and *Clidemia hirta*), occurs between 450 and 600 m a.s.l.

The canopy is stunted (4–6 m) in height and open (10–40%) in cover; the understory is dense (100% cover). The stunted *Metrosideros* trees are of vegetatively low vigor, with dead or defoliated branches. Their roots are restricted to a few centimeters of surface soils or directly abut on the soil surface and are covered only by mosses. Such trees are typically stilted by aerial roots. The same trees, on the other hand, show reproductive vigor, producing abundant flowers. However, regeneration is only sporadic, probably due to the paucity of such substrates as fallen logs, on which seedlings can establish themselves, as stated also by Holt (1988). *Dicranopteris linearis* and *A. virginicus* dominate the ground. Weeds are abundant both in cover and species number. In the differential species group, *A. virginicus*, *P. cattleianum*, and *C. hirta* are listed among the 12 worst weeds in Hawaii's national parks by Smith (1990).

The community lies entirely in the dieback area, initially described by Lyon (1909) and more recently by Holt (1983, 1988). Dieback is widespread on the lowland flat interfluve along the transect. This stunted plant community, which is underlain by saturated soils with thick moss layers, is a consequence of forest dieback associated with soil deterioration for native tree growth (Holt 1988). There is a possibility that the stand reduction due to dieback in turn further aggravates the soil waterlogging (Mueller-Dombois 1988*b*). The moss layers develop a peculiar mound-forming microtopography like a high moor. A similar process of a more recent stand-reduction dieback on Mauna Kea with soil degradation was termed bog formation dieback by Mueller-Dombois et al. (1977) and Mueller-Dombois (1980).

A2. *M. polymorpha* var. *glaberrima–Adenophorus pinnatifidus* community (intact lowland zone, partially open to closed canopy evergreen rainforest) (see Figure 4*b*)

The *M. polymorpha* var. *glaberrima–Adenophorus pinnatifidus* community is differentiated by six endemic species (*Adenophorus pinnatifidus*, *Psychotria mariniana*, *Peperomia obovatilimba*, *P. hirtipetiola*, *Syzygium sandwicensis*, and *Labordia hedyosmifolia*) and two indigenous species (*Freycinetia arborea* and *Diplopterygium pinnatum*). Most stands of this community occur between 600 and 1000 m a.s.l. with the exception of a few stands on lower ridge crests at 350 m, where lateral drainage is better than on the surrounding flat interfluves. The lower ridge crests support the better preserved forest fragments in the dieback territory.

The vegetation is low to tall (7–12 m) and widely open to closed (30–80% canopy cover). The shrub layer is 5 m tall, sparse to dense (30–80% cover), and dominated by *Dicranopteris linearis*, *Cibotium chamissoi*, and *C. glaucum*. The herb layer is 1 m tall, sparse to dense (20–100% cover), and, on imperfectly drained soils, is dominated by the same species as those of the shrub layer, or by *Paspa-*

FIGURE 4. Views of the lower transect communities: *a*, lowland dieback community (unit A1 in Appendix) at 450 m, showing remaining dead snags of *Metrosideros*; *b*, lowland intact forest (A2) at 800 m; *c*, canopy layer of the lower and upper montane forests (B1 and B2) viewed from 1350 m.

lum conjugatum, *Cyperus halpan*, and *Juncus planifolius* on saturated soils. Trees become progressively mossy, and epiphytic ferns become abundant toward the upper limit.

B. *Vaccinium calycinum* unit (montane zone)

The *Vaccinium calycinum* unit is distributed in the middle segment of the slope between 1200 and 1950 m a.s.l., corresponding to the montane zone. Eight endemic species (*V. calycinum*, *Elaphoglossum wawrae*, *Coprosma ochracea*, *Rubus hawaiensis*, *Dryopteris subbipinnata*, *D. glabra*, *Ctenitis rubiginosa*, and *Adenophorus tripinnatifidus*) and two indigenous species (*Dryopteris wallichiana* and *Uncinia uncinata*) differentiate this unit.

Three plant communities are distinguished in this unit: B1, *M. polymorpha* var. *glaberrima–Nertera granadensis* community; B2, *M. polymorpha* var. *glaberrima–Pelea clusiifolia* community; and B3, *M. polymorpha* var. *glaberrima–Sadleria cyatheoides* community. These three communities correspond to three subzones, the lower montane zone (B1), the upper montane zone (B2), and the forest line (B3).

B1. *M. polymorpha* var. *glaberrima–Nertera granadensis* community (lower montane zone, closed canopy evergreen moss forest) (see Figure 4*c*)

The *M. polymorpha* var. *glaberrima–Nertera granadensis* community, differentiated by 11 endemic taxa (*M. polymorpha* var. *incana*, *Peperomia expallescens*, *P. macraeana*, *Xiphopteris saffordii*, *Labordia venosa*, *Cyrtandra hashimotoi*, *Adenophorus montanus*, *Psychotria hawaiiensis*, *Cyrtandra platyphylla*, *Thelypteris sandwicensis*, and *Dryopteris acutidens*) and three indigenous species (*Nertera granadensis*, *Grammitis hookeri*, and *Korthalsella complanata*), occurs between 1200 and 1700 m a.s.l. Clouds persistently envelope this altitudinal zone. Consequently, epiphytic mosses and ferns grow abundantly in all strata, forming mossy forests. *Metrosideros polymorpha* var. *incana* (a pubescent variety of *M. polymorpha*) intermixes with *M. polymorpha* var. *glaberrima* with various degrees of cover in the canopy. Both varieties are sclerophyllous. Sclerophylly may be related primarily to the oligotrophic montane soils as suggested by Grubb (1977), or to the highly saturated air, which retards transpiration and in turn nutrient uptake (Leigh 1975).

The canopy is tall (10–15 m) and closed or partially open. The shrub layer (3–5 m tall) is generally dense (50 to 80% cover); there is no single dominant shrub species, however *Vaccinium dentatum*, *V. calycinum*, *Broussaisia arguta*, and the forb *Astelia menziesiana* are abundant. The herb layer is dense (near 90% cover) and dominated by *Carex alligata* on saturated soils. It becomes sparser (less than 70%) and more mixed with other herbaceous species on somewhat better drained soils. Epiphytic ferns (*Elaphoglossum hirtum*, *E. wawrae*, *Mecodium recurvum*, *Sphaerocionium lanceolatum*), terrestrial ferns (*Dryopteris* and *Asplenium*), and *Peperomia* are abundant among low-growing shrub species in the herb layer. Invasion by alien weeds is rarely seen in most stands. However, along the flume, where the forests were cleared and regularly visited, alien graminoids such as *Juncus planifolius* are abundant. The canopy trees of *Metrosideros* show even-sized boles. Canopy dieback is locally evident in this montane zone where soils are saturated, but dieback stands are not distinguishable floristically from intact ones in the differential table.

B2. *M. polymorpha* var. *glaberrima–Pelea clusiifolia* community (upper montane zone, closed canopy evergreen rainforest) (see Figure 4*c*)

The *M. polymorpha* var. *glaberrima–Pelea clusiifolia* community, differentiated by three endemic species (*P. clusiifolia*, *Asplenium normale*, and *Peperomia membranacea*), occurs between 1750 and 1950 m a.s.l. This community marks the upper limit of closed forest beyond which forest canopies become open. The mosses no longer prevail, and epiphytic mosses are largely replaced by lichens. The canopy layer is tall (15 m) and closed. *Acacia koa* becomes codominant near the upper limit of the community range (1900 m a.s.l.). The canopy trees are ground-rooted, unlike those at lower elevation. The shrub layer is sparse (5% cover); *Coprosma ochracea*, *Vaccinium calycinum*, and *P. clusiifolia* are frequently encountered. The herb layer is dense (100% cover), predominated by *Athyrium sandwichi-*

anum interspersed with other terrestrial ferns such as *Dryopteris*, *Asplenium*, and *Ctenitis*. The dense fern layer and the occurrence of ground-rooted trees are related to the well-drained soils. Invasion by weeds into the community is scarcely seen.

B3. *M. polymorpha* var. *glaberrima–Sadleria cyatheoides* community (forest line, ecotone community between the upper montane forest and the subalpine scrub) (see Figure 5*a*)

The *M. polymorpha* var. *glaberrima–Sadleria cyatheoides* community occurs at the forest line between 1900 and 1950 m a.s.l. The differential species group includes four endemic taxa: *Sadleria cyatheoides*, *M. polymorpha* var. *polymorpha*, *Oreobolus furcatus*, and *Polystichum bonseyi*. The forest structure consists of a low (5–8 m tall) and partially to widely open canopy layer (5–60% cover) and a dense herb layer (70–100% cover). *M. polymorpha* var. *polymorpha* (a tomentose-leaved variety of *M. polymorpha*) intermixes with *M. polymorpha* var. *glaberrima* in the canopy at the lower limit of the community, but forms pure stands at the upper limit. *Acacia koa* is another canopy tree species that becomes abundant locally. The herb layer is dominated by either *Dryopteris wallichiana* or *S. cyatheoides*, with two alien grass species (*Anthoxanthum odoratum* and *Holcus lanatus*) as codominants. The community can be considered an ecotone between the closed upper montane forest and the subalpine scrub. Several subalpine elements such as *Vaccinium reticulatum*, *Coprosma ernodeoides*, and *Deschampsia nubigena* consistently occur in the community.

II. Treeless Vegetation

C. *Dubautia menziesii* unit (high-altitude zone)

Sparse vegetation characterizes the landscape above 1950 m a.s.l. Mutually exclusive with the forest vegetation, a single endemic species differentiates the *Dubautia menziesii* unit, which lies entirely in the subalpine and alpine treeless vegetation (Figure 3).

Tall trees are absent from this vegetation type. The only exception are widely scattered *M. polymorpha* var. *polymorpha* trees, which range from the forest line to the tree line at 2200 m a.s.l.

This unit contains the following two plant communities, which are physiognomically and floristically distinct: C1, *Sophora chrysophylla* community and C2, *Tetramolopium humile* community.

C1. *Sophora chrysophylla* community (subalpine zone, tropical subalpine scrub) (see Figure 5*b*)

The *Sophora chrysophylla* community, differentiated by three endemic shrubs (*S. chrysophylla*, *Coprosma montana*, and *Geranium cuneatum* ssp. *tridens*) and one endemic sedge (*Carex wahuensis*), occurs between 1950 and 2700 m a.s.l. The canopy shrub layer is low (1.5–3 m in height) and widely open (5–50% cover). The herb layer is relatively dense (40–90% cover). The differential shrub species and *Styphelia tameiameiae* prevail in the shrub layer. In the herb layer, endemic species (*Dubautia menziesii*, *Coprosma ernodeoides*, *Deschampsia nubigena*, *Vaccinium reticulatum*, and *Luzula hawaiiensis*) and alien species (*Hypochoeris radicata*, *Anthoxanthum odoratum*, and *Holcus lanatus*) are prevalent. The community shows some xeromorphic adaptations to the arid environment, as reflected in sclero-microphylly.

The community is further subdivided into two subunits: C1a, *Prunella vulgaris* subunit and C1b, *Trisetum glomeratum* subunit. The *P. vulgaris* subunit is differentiated by *Prunella vulgaris*, *Epilobium billardierianum* ssp. *cinereum*, and *Coprosma ernodeoides*. These species occur in the lower segment of the subalpine zone (1950–2400 m a.s.l.). The *T. glomeratum* subunit is differentiated by *Trisetum glomeratum*, *Rumex acetosella*, *Pellaea ternifolia*, *Asplenium adiantum-nigrum*, *A. trichomanes*, and *Dodonaea viscosa*, occurring at higher elevation (2300–2700 m a.s.l.) and marking the shrub line.

C2. *Tetramolopium humile* community (alpine zone, tropical alpine desert) (see Figure 5*c*)

The *Tetramolopium humile* community, differentiated by two endemic species (*T. humile* ssp. *haleakalae* and *Argyroxiphium sandwicensis* ssp. *macrocephalum*), occurs above 2700 m a.s.l. The substrates are pyroclastic ashes

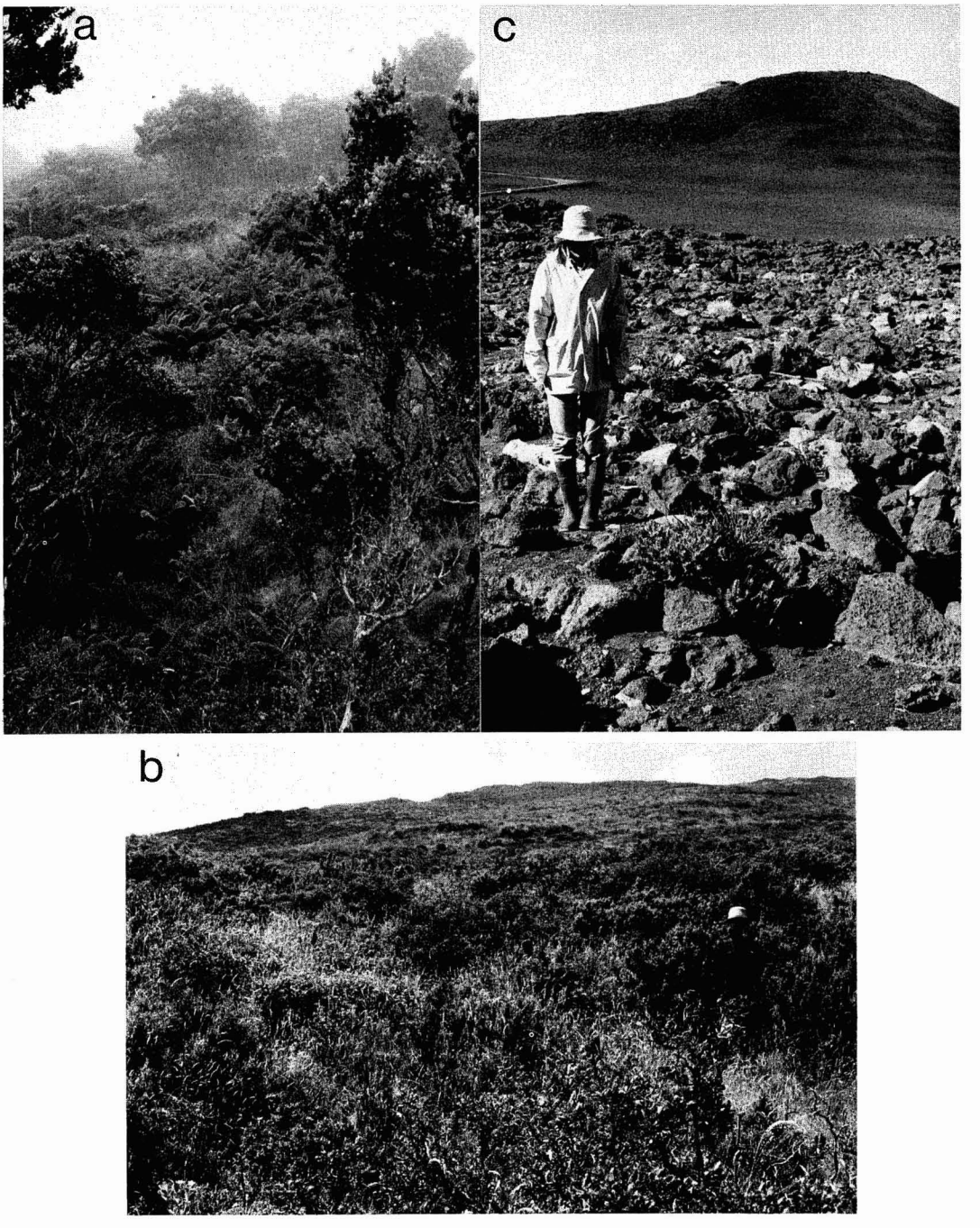

FIGURE 5. Views of the upper transect communities: *a*, forest line (unit B3 in Appendix) at 1950 m; *b*, lower subalpine scrub (C1a) at 2100 m; *c*, alpine desert (C2) near the summit.

and rocks. The community is very sparse, with less than 5% cover, low (<1 m in height except when *Argyroxiphium* flowers), and rather barren in physiognomy. *A. sandwicensis* ssp. *macrocephalum* (silversword) is a monocarpic giant rosette of the Compositae, a characteristic life form of tropical alpine zones elsewhere (e.g., in the afroalpine zones and the Andean mountains). The other constituents include the native species *Dubautia menziesii*, *Trisetum glomeratum*, *Asplenium adiantum-nigrum*, *A. trichomanes*, *Styphelia tameiameiae*, and *Deschampsia nubigena* and one alien species, *Hypochoeris radicata*.

Species Richness along the Transect

The numbers of species in the communities are shown in Table 1. The total number of species per community ranges from 14 in the alpine desert (unit C2 in the Appendix) to 103 species in the lower montane forest (B1). The mean species number per stand ranges from 7.3 species (4–10) in the alpine desert to 43.5 species (31–55) in the lower montane forest.

The lower montane forest is relatively more diverse in flora than the lowland intact forest (A2). The lowland dieback community (A1) has a lowered species richness (21 species per stand), comparable to that of the forest line community (B3, 23.2 species per stand).

Relationships between the Classified Communities

Figure 6 depicts community relationships among the eight classified units in the form of a dendrogram. The hierarchical ranking shown in the Appendix was based on the selection of diagnostic species, but the relationships depicted in Figure 6 are based on the species quantities of all constituents in each unit. The calculation of community similarities is based on species constancy values (%) per unit, using Sørensen's similarity index modified for quantitative application (Mueller-Dombois and Ellenberg 1974):

$$IS = 2Mw/(MA + MB)$$

where Mw = sum of the smaller constancy

TABLE 1

SPECIES RICHNESS OF THE CLASSIFIED PLANT COMMUNITIES

Total number of plant species per community and mean species number per stand for each community are shown. The communities are indicated by codes:

A1. Lowland dieback (*M. polymorpha* var. *glaberrima–O. chinensis* community)
A2. Lowland intact forest (*M. polymorpha* var. *glaberrima–A. pinnatifidus* community)
B1. Lower montane forest (*M. polymorpha* var. *glaberrima–N. granadensis* community)
B2. Upper montane forest (*M. polymorpha* var. *glaberrima–P. clusiifolia* community)
B3. Forest line (*M. polymorpha* var. *glaberrima–S. cyatheoides* community)
C1a. Lower subalpine scrub (*S. chrysophylla* community, *P. vulgaris* subunit)
C1b. Upper subalpine scrub (*S. chrysophylla* community, *T. glomeratum* subunit)
C2. Alpine desert (*T. humile* community)

	LOWLAND		MONTANE			HIGH ALTITUDE		
PLANT COMMUNITY	A1	A2	B1	B2	B3	C1a	C1b	C2
Total number	47	100	103	52	56	28	26	14
Mean per stand	21	38.4	43.5	24.7	23.2	14.2	15.2	7.3
(Range)	19–25	14–54	31–55	15–31	13–32	11–17	11–18	4–10

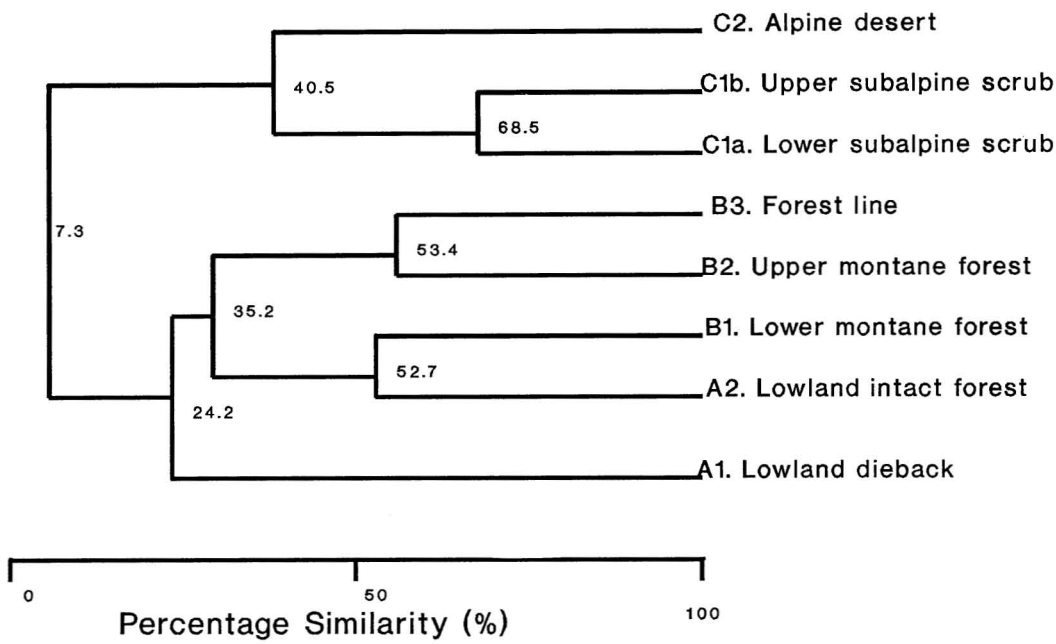

FIGURE 6. Dendrogram analysis applied to the classified plant communities on the windward slope of Haleakala.

values of the species common to two communities; MA and MB = sum of the constancy values of all species in each of the two communities.

Overall, the communities share relatively high similarities despite the differences in their environments. The lower subalpine scrub (unit C1a in the Appendix) and the upper subalpine scrub (C1b) have the highest similarity since they are subunits of the same community. The lowland intact forest (A2) has a higher similarity with the lower montane forest (B1) than with the lowland dieback community (A1), although A1 and A2 are parts of the same unit in the hierarchy (Appendix 1 and Figure 3). This is because the lowland intact forest shares more species with the lower montane forest than with the lowland dieback community. The lowland dieback community has low similarities with any of the intact forest communities (A2, B1, B2, and B3) (joining them at the level of 24.2%), suggesting that canopy dieback in that zone impoverished the species composition.

The similarity between the alpine (C2) and subalpine (C1a and C1b) communities is relatively high despite the low species richness of the alpine community. Several common alien species, spanning both zones, are responsible for this high similarity.

DISCUSSION

Altitudinal Zonation

Previous workers (Egler 1939, Krajina 1963, Knapp 1965, Mueller-Dombois and Spatz 1981, and Gagné and Cuddihy 1990) have variously described and characterized altitudinal vegetation zones of the Hawaiian Islands. The results of the strictly floristically defined study reported here show altitudinal zones comparable to those of Knapp (1965), Mueller-Dombois and Spatz (1981), and Gagné and Cuddihy (1990). Moreover, the number of altitudinal zones agrees with those described for continental tropical high mountains by Grubb (1974), who used vegetation structure and physiognomy as the principal classifying criteria.

An important difference from the previous studies is the hierarchical arrangement of vegetation in this study. In descending order

of the hierarchy, two major species groups have defined the two broadest ecological zones that split at the trade wind inversion. At the second level, three floristic units define the lowland, the montane, and the high-altitude (subalpine and alpine) zones. At the third level, seven plant communities and two additional subunits within one of the communities designate finer altitudinal zones (Figure 3). Of these communities, the *M. polymorpha* var. *glaberrima–Odontosoria chinensis* community defines the lowland dieback belt. This is considered a retrogressive variation of the lowland rainforest zone, because the impoverishment of native species and invasion of aliens seem to be a direct consequence of canopy dieback.

Species groups that differentiate lower units in descending order of the hierarchy consist mostly of herb and shrub species (except *Syzygium sandwicensis* and *M. polymorpha* var. *incana*), while canopy tree species segregate the forest from the nonforest vegetation. Therefore, any finer altitudinal differentiation in the forest vegetation is floristically recognizable only by understory species. This fact contrasts with the situation in continental tropical mountains where zonal differentiation is often evident through changes in canopy species composition (Whitmore 1975).

The upper limits of the subalpine and montane zones on Haleakala are similar to those on Mauna Loa (Mueller-Dombois and Spatz 1981) on the neighboring island of Hawaii. This is so in spite of the montane segment studied on Mauna Loa being "seasonal," and thus different from the year-round perhumid montane environment on Haleakala. Moreover, the montane seasonal environment on Mauna Loa is dominated by *Acacia koa*, while on Haleakala there is a narrow belt of *Acacia koa* where the upper montane zone changes into the subalpine zone. In the subalpine zone, *Metrosideros* trees are more abundant on Mauna Loa than on Haleakala. When compared with that of a higher mountain of the same floristic region, vegetation of a lower mountain is often telescoped into depressed, narrower zones than those of the higher mountain. Despite the differences in the dominance type and in the summit height (ca. 1000 m), major species turnover points occur at the same altitudes on both mountains (i.e., the upper limits of the montane and subalpine zones).

In comparison to the high mountains of Malesia, with which the Hawaiian islands have some floristic affinity (Wagner et al. 1990), the limits of subalpine and alpine zones of Haleakala are more than 1000 m lower than those of Malesian mountains (except on recent Malesian volcanoes). The difference is especially evident when forest lines are compared: the forest line of Mt. Wilhelm (4672 m) in Papua New Guinea is at 3900 m a.s.l. (Wade and McVean 1969), that of Mt. Kinabalu (4101 m) in Borneo is at 3700 m a.s.l. (Kitayama 1987), while that of Haleakala is only at 1950 m. The forest line of Mt. Kinabalu coincides with the daily ground-frost line; that of Mt. Wilhelm is found above the daily ground-frost line. On Haleakala the ground-frost line (2700 m a.s.l.) coincides with the lower limit of the alpine zone, which is 700 m above the forest line.

The two Malesian mountains (Wilhelm and Kinabalu) were uplifted between the late Pliocene and the early Pleistocene. They are rather similar in geological age to Haleakala, which originated in the late Pleistocene. The Malesian mountains are, however, said to support a more harmonic flora and are definitely much richer in species than is Haleakala. One reason for the zonal depression is probably related to floristic differences. For instance, the Hawaiian flora lacks podocarpaceous tree species, which are dominant subalpine elements in circum-Pacific regions of the Southern Hemisphere (Troll 1958). In addition, it seems that no highland-adapted tree species, which are tolerant of the cold and arid environment, have evolved on the Hawaiian mountains. This may be due to some evolutionary constraints of Hawaiian tree species (e.g., no highland-adapted *Syzygium* is found in Hawaii).

Species Turnover

On Haleakala, altitudinal species turnover, which is the compositional change along an altitudinal gradient by spatial species displacements, is exceedingly low despite the diverse habitat types along the transect. The

low species turnover stems from the fact that many species are associated over broad altitudinal ranges. For instance, 20 species are associated and range from the lowland to the forest line (*M. polymorpha* var. *glaberrima* group in Figure 3).

The boundary between the *M. polymorpha* var. *glaberrima* group and the *D. menziesii* group (Figure 3) shows an abrupt species turnover. However, several species range across the boundary formed by the two major species groups. These species are represented by *Styphelia tameiameiae*, which shows the most individualistic distribution and spans from the lower montane zone to the summit area without associated species (see Appendix). Consequently, such unassociated species lower somewhat the otherwise high turnover rate between the two species groups. This low species turnover along the mountain slope may be considered a characteristic of isolated island mountains.

Altitudinal Conspecific/Generic Segregation

Subdivisions of the forest vegetation were recognizable notably by the species of the understory. However, our results also show an incipient canopy tree segregation: a conspecific segregation of *M. polymorpha* into zonal varieties. *Metrosideros polymorpha* is present with three morphological varieties along the transect (Figure 7). Of these, var. *glaberrima* occupies the broadest range. Overlapping with this, var. *incana* is confined to the lower montane zone. Var. *polymorpha* is sharply separated from the first variety, and occurs above the inversion. Stemmermann (1983) stated that the pubescent character,

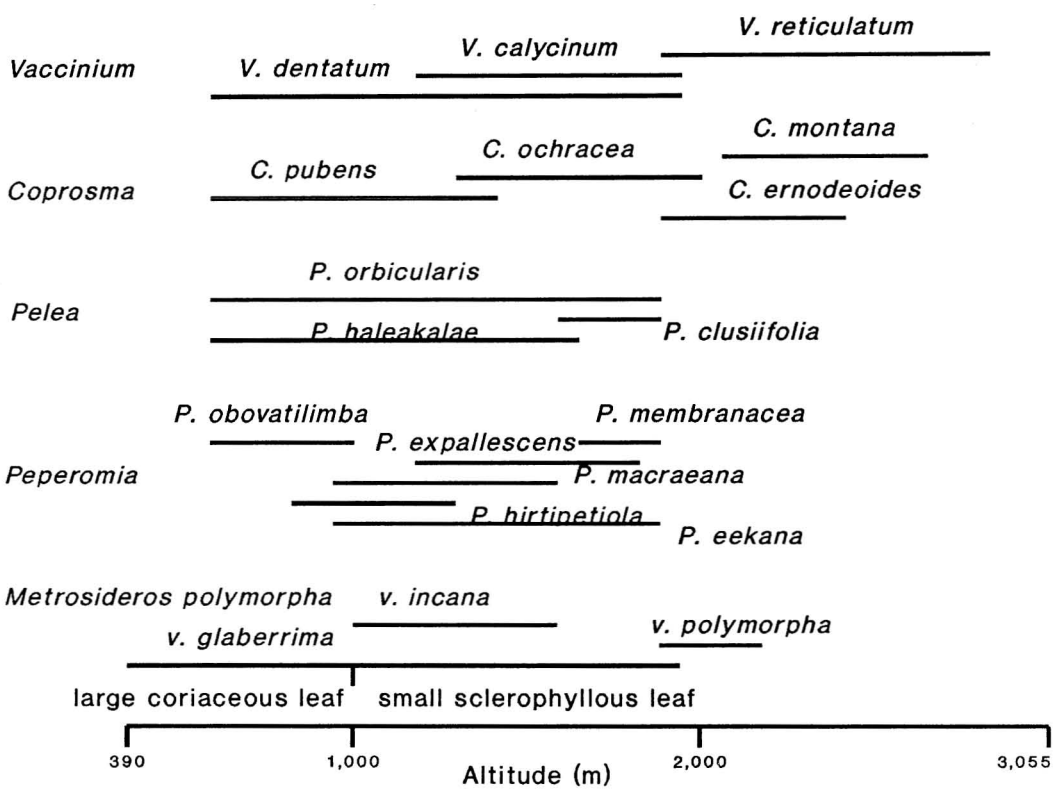

FIGURE 7. Altitudinal distribution patterns of selected conspecific/congeneric taxa along the transect.

which is a principal morphological distinction for the varieties, is genetically fixed.

Moreover, within the glabrous variety (*glaberrima*) a large coriaceous leaf variant and a small sclerophyllous leaf variant are discernable, although not recognized by taxonomists. These morphological leaf variants are dissociated from each other in distribution, and respectively confined to the lowland and to the montane zone. The leaf variants may be ecotypic (Corn and Hiesey 1973) and are likely in the process of altitudinal segregation.

In addition to *Metrosideros*, altitudinal segregation of mutually related taxa is commonly seen also at the specific level. Examples of genera showing such species segregations along the altitudinal gradient include *Coprosma*, *Vaccinium*, *Asplenium*, *Peperomia*, *Adenophorus*, *Dryopteris*, and *Pelea*. Among these, the genera *Coprosma*, *Vaccinium*, and *Asplenium* have exceedingly broad ranges: 600–2700 m, 600–2800 m, and 600–3000 m a.s.l., respectively. Figure 7 depicts altitudinal species distributions of a few representative angiosperm genera. In these genera, constituent species are probably genetically closely related. Morphological resemblance and mutually exclusive distributions in *Pelea haleakalae* and *P. clusiifolia*, and in *Coprosma pubens*, *C. ochracea*, and *C. montana* indicate their vicarious or ecotypic relationships.

Congeneric segregation has also been reported from the Mauna Loa transect study (Mueller-Dombois 1981*b*). Such segregations are also found on upper slopes of continental tropical mountains (e.g., altitudinally vicarious afroalpine species [Hedberg 1986] and adaptive altitudinal radiation [Lee and Lowry 1980]). The examples on the oceanic islands relate to the invasion and subsequent adaptation to mountains volcanically emerged from the ocean (Carlquist 1974), while those on the continental mountains appear to be related to the upward adaptation to the postglacial high-altitude environment.

Community Organization

This floristic analysis, applied to an isolated oceanic-island mountain with a biologically impoverished flora, has unexpectedly resulted in altitudinal zones similar in number to those found on species-rich mountains. The implication is that factors controlling the zonal vegetation patterns and their limits are predominantly climatic since the differential species are well correlated with altitude. Temperature lapse rates are probably a chief determinant because air temperature consistently decreases upslope independently of other factors on both continental and oceanic-island mountains. On Haleakala, moisture is another important factor, as reflected in the sharp boundary at the inversion.

Grubb (1977) discussed causative factors of tropical mountain zonation. He suggested that the upper limits of species are set primarily by temperature and the lower limits by competition. He further suggested that other adverse effects such as soil nutrient deficiencies, waterlogging, and reduced light in the cloud zone depress the potential distribution limits.

The question of whether lower limits are set by competition is intricate. This question can only be resolved by an experimental approach. Distribution analysis can only suggest a mechanism. In our example, *Styphelia tameiameiae*, which has the most individualistic distribution, seems little affected by species competition, while the lower limit of the heliophytic subalpine species *Coprosma ernodeoides* appears to be controlled by competition with montane trees. *Coprosma ernodeoides* is occasionally found farther downslope in anthropogenically cleared areas. Recurrence of the same endemic shrub taxa at high and low elevations has also been recorded along the Mauna Loa transect. There, the double occurrence was attributed to the natural openness associated with pioneer habitats (Mueller-Dombois and Spatz 1981).

Whittaker (1975) suggested that the distribution of species along an environmental gradient is a function of both adaptation and competition. He further suggested that the evolving patterns of species packing result in increasingly narrower distribution ranges with random assortment of individual species rather than associated species patterns. The study on Haleakala reported here has shown that a large number of species assemble in

associated patterns, confirming an earlier study done on Mauna Loa during the IBP project (Mueller-Dombois 1981*c*).

One of the associations is indicative of invading patterns of alien species due to canopy dieback (i.e., the *Odontosoria chinensis* group, which largely consists of aliens). The associations consisting mostly of native species are variously distributed in range.

Evolutionary processes of radiation may progress spatially in two scenarios: A group of generalistic species may assemble over a broad range limited only by environmental constraints. Subsequently, the individual taxa split by evolutionary adaptation into related congeneric taxa with narrower amplitudes. The second scenario involves species invasion with slow range expansion accompanied by adaptation.

An initially low species packing may allow the first process of generalist expansion to be more prevalent. In contrast, where species packing has advanced to a higher degree, invasion of new species is expected to proceed less explosively, and subsequent range extensions can only occur by adaptive changes or competitive displacement of other taxa. The overall outcome is the same. However, since this study revealed a large number of species with broad-ranging distribution patterns, it seems likely that the first scenario is more typical for island mountains, where interspecific competition is initially only a minor constraint.

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APPENDIX

SUMMARIZED DIFFERENTIAL TABLE OF THE VEGETATION ON THE WINDWARD SLOPE OF HALEAKALA, MAUI, HAWAII

Figures are constancy values (%) per vegetation unit. **, alien species; *, indigenous species; unmarked, endemic species.

Forest Vegetation

A. *Elaphoglossum crassifolium* unit
  A1. *M. polymorpha* var. *glaberrima–O. chinensis* community
  A2. *M. polymorpha* var. *glaberrima–A. pinnatifidus* community

B. *Vaccinium calycinum* unit
  B1. *M. polymorpha* var. *glaberrima–N. granadensis* community
  B2. *M. polymorpha* var. *glaberrima–P. clusiifolia* community
  B3. *M. polymorpha* var. *glaberrima–S. cyatheoides* community

Treeless Vegetation

C. *Dubautia menziesii* unit
  C1. *Sophora chrysophylla* community
    C1a. *Prunella vulgaris* subunit
    C1b. *Trisetum glomeratum* subunit
  C2. *Tetramolopium humile* community

PLANT COMMUNITY CODE NUMBER OF RELEVÉS	A1 8	A2 19	B1 23	B2 9	B3 12	C1a 16	C1b 13	C2 11
Differential species of the forest vegetation *Metrosideros polymorpha* var. *glaberrima*	100	100	100	100	75	0	0	0
Cheirodendron trigynum	0	95	100	100	75	0	0	0
Vaccinium dentatum	0	95	100	67	17	0	0	0
Myrsine lessertiana	0	58	96	78	50	0	0	0
*Elaphoglossum hirtum**	13	53	91	100	33	0	0	0
Broussaisia arguta	0	79	100	33	0	0	0	0

PLANT COMMUNITY CODE NUMBER OF RELEVÉS	A1 8	A2 19	B1 23	B2 9	B3 12	C1a 16	C1b 13	C2 11
Athyrium microphyllum	0	26	100	44	58	0	0	0
Hedyotis (Gouldia) terminalis	0	74	87	11	0	0	0	0
Astelia menziesiana	0	47	100	11	8	0	0	0
Sadleria pallida	0	53	87	22	17	0	0	0
Carex alligata	0	5	70	56	67	6	0	0
Polypodium pellucidum	0	26	87	44	17	0	0	0
*Asplenium polyodon**	13	32	57	89	17	0	0	0
Myrsine sandwicensis	0	63	70	22	0	0	0	0
Athyrium sandwichianum	0	42	44	100	17	0	0	0
*Ilex anomala**	13	47	52	22	25	0	0	0
*Pleopeltis thunbergiana**	38	16	39	78	33	0	0	0
Smilax sandwicensis	0	58	44	11	8	0	0	0
*Asplenium lobulatum**	0	37	44	33	0	0	0	0
*Rubus argutus***	0	47	4	11	75	0	0	0
Differential species of C								
Dubautia menziesii	0	0	0	0	0	50	100	100
Differential species of A								
Elaphoglossum crassifolium	88	95	0	0	0	0	0	0
*Paspalum conjugatum***	100	68	0	0	0	0	0	0
Adenophorus hymenophylloides	63	58	13	0	0	0	0	0
*Psilotum complanatum**	38	68	4	0	0	0	0	0
Antidesma platyphyllum	63	47	0	0	0	0	0	0
Tetraplasandra oahuensis	13	58	9	0	0	0	0	0
*Cyperus halpan***	50	47	0	0	0	0	0	0
*Huperzia phyllanthum**	63	42	0	0	0	0	0	0
*Nephrolepis cordifolia**	25	58	0	0	0	0	0	0
*Rubus rosifolius***	25	47	9	0	0	0	0	0
*Psilotum nudum**	38	32	0	0	0	0	0	0
*Setaria palmifolia***	13	42	0	0	0	0	0	0
Differential species of B								
Vaccinium calycinum	0	0	96	100	83	0	0	0
*Dryopteris wallichiana**	0	0	91	89	83	25	0	0
Elaphoglossum wawrae	0	0	100	100	50	0	0	0
Dryopteris glabra	0	0	61	89	58	0	0	0
Coprosma ochracea	0	0	39	100	83	0	0	0
Rubus hawaiensis	0	0	30	89	83	0	0	0
*Uncinia uncinata**	0	0	61	78	33	0	0	0
Ctenitis rubiginosa	0	0	44	100	17	0	0	0
Dryopteris subbipinnata	0	0	4	78	42	0	0	0
Adenophorus tripinnatifidus	0	0	26	44	8	0	0	0
Differential species of A1								
*Odontosoria (Sphenomeris) chinensis**	100	11	0	0	0	0	0	0
*Andropogon virginicus***	88	16	0	0	0	0	0	0
*Psidium cattleianum***	88	5	0	0	0	0	0	0
*Centella asiatica***	75	5	0	0	0	0	0	0
*Sacciolepis indica***	50	16	0	0	0	0	0	0
*Tibouchina herbacea***	75	0	0	0	0	0	0	0
*Clidemia hirta***	50	5	0	0	0	0	0	0
*Machaerina mariscoides meyenii**	25	0	0	0	0	0	0	0
Differential species of A2								
Adenophorus pinnatifidus	0	84	4	0	0	0	0	0
*Freycinetia arborea**	0	63	13	0	0	0	0	0
Psychotria mariniana	0	68	0	0	0	0	0	0
Peperomia obovatilimba	0	63	4	0	0	0	0	0
Syzygium sandwicensis	0	58	0	0	0	0	0	0
Peperomia hirtipetiola	0	42	13	0	0	0	0	0

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*Diplopterygium pinnatum**	0	42	17	0	0	0	0	0
Labordia hedyosmifolia	0	26	0	0	0	0	0	0
Differential species of B1								
*Nertera granadensis**	0	0	100	11	0	0	0	0
Peperomia expallescens	0	0	91	11	0	0	0	0
Metrosideros polymorpha var. *incana*	0	16	78	0	0	0	0	0
Peperomia macraeana	0	16	74	0	0	0	0	0
Xiphopteris saffordii	0	11	74	0	0	0	0	0
*Grammitis hookeri**	0	0	78	0	0	0	0	0
Cyrtandra hashimotoi	0	11	65	0	0	0	0	0
Labordia venosa	0	0	74	0	0	0	0	0
Adenophorus montanus	0	0	65	0	0	0	0	0
Psychotria hawaiiensis	0	0	65	0	0	0	0	0
Cyrtandra platyphylla	0	11	52	0	0	0	0	0
*Korthalsella complanata**	0	16	44	0	0	0	0	0
Thelypteris sandwicensis	0	0	39	0	0	0	0	0
Dryopteris acutidens	0	0	30	0	0	0	0	0
Differential species of B2								
Pelea clusiifolia	0	0	22	78	0	0	0	0
*Asplenium normale**	0	0	4	56	8	0	0	0
Peperomia membranacea	0	0	4	56	8	0	0	0
Differential species of B3								
Sadleria cyatheoides	0	0	0	33	100	0	0	0
Metrosideros polymorpha var. *polymorpha*	0	0	0	0	83	13	0	0
Oreobolus furcatus	0	0	0	0	42	0	0	0
Polystichum bonseyi	0	0	0	0	33	0	0	0
Differential species of A2 and/or B1								
Cibotium chamissoi	38	100	91	0	0	0	0	0
Mecodium recurvum	75	90	65	0	0	0	0	0
Adenophorus tamariscinus	88	90	61	0	0	0	0	0
Grammitis tenella	88	79	48	0	0	0	0	0
Cibotium glaucum	75	100	96	0	0	0	0	0
*Dicranopteris linearis**	100	79	61	0	0	0	0	0
*Lycopodium cernuum**	100	68	22	0	0	0	0	0
Dryopteris tetrapinnata	0	5	22	0	0	0	0	0
Liparis hawaiensis	0	16	26	0	0	0	0	0
Dryopteris nuda	0	16	35	0	0	0	0	0
Pelea haleakalae	0	84	87	0	0	0	0	0
Sphaerocionium lanceolatum	0	84	70	0	0	0	0	0
Clermontia arborescens waihiae	0	84	65	0	0	0	0	0
Elaphoglossum alatum	0	74	44	0	0	0	0	0
Alyxia oliviformis	0	58	57	0	0	0	0	0
Pelea orbicularis	0	47	52	0	8	0	0	0
*Juncus planifolius***	0	47	22	0	0	0	0	0
Stenogyne rotundifolia	0	21	22	11	8	0	0	0
Wikstroemia monticola	0	37	30	0	0	0	0	0
Vandenboschia cyrtotheca	0	21	9	0	0	0	0	0
*Machaerina angustifolia**	0	26	4	0	0	0	0	0
Hedyotis (*Gouldia*) *hillebrandii*	0	21	9	11	0	0	0	0
Coprosma pubens	0	32	9	0	0	0	0	0
Differential species of C1								
Sophora chrysophylla	0	0	0	0	0	94	100	0
Coprosma montana	0	0	0	0	0	81	100	0
Geranium cuneatum tridens	0	0	0	0	0	88	62	0
Carex wahuensis	0	0	0	0	0	63	39	0

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Differential species of C2								
Tetramolopium humile haleakalae	0	0	0	0	0	0	0	100
Argyroxiphium sandwicensis macrocephalum	0	0	0	0	0	0	0	64
Differential species of C1b								
Trisetum glomeratum	0	0	0	0	0	0	92	82
*Rumex acetosella***	0	0	0	11	33	38	92	0
*Pellaea ternifolia**	0	0	0	0	0	0	62	9
*Asplenium adiantum-nigrum**	0	0	0	0	0	0	46	36
*Asplenium trichomanes**	0	0	0	0	0	0	31	46
*Dodonaea viscosa**	0	0	0	0	0	0	23	0
Differential species of C1a and/or B3								
*Epilobium billardierianum cinereum***	0	0	0	0	17	50	0	0
*Prunella vulgaris***	0	0	0	0	58	69	0	0
Coprosma ernodeoides	0	0	0	0	58	50	0	9
*Hypochoeris radicata***	0	0	0	0	83	100	100	91
Deschampsia nubigena	0	0	9	0	67	81	100	82
Vaccinium reticulatum	0	0	0	0	83	100	92	18
*Anthoxanthum odoratum***	0	0	4	22	83	100	62	0
Pteridium aquilinum var. *decompositum**	0	0	0	0	42	100	100	0
*Holcus lanatus***	0	0	4	0	58	100	54	0
Luzula hawaiiensis	0	0	0	0	33	44	85	18
Lycopodium venustulum	0	11	4	0	33	6	0	0
Unclassified species								
*Styphelia tameiameiae**	0	0	100	89	92	100	100	46
Peperomia eekana	0	5	26	22	0	0	0	0
*Erechtites valerianifolia***	13	32	4	0	0	0	0	0
Acacia koa	13	0	0	33	25	0	0	0
*Lapsana communis***	0	0	0	11	25	0	23	0
Stenogyne kamehamehae	0	11	13	11	0	0	0	0
Dryopteris unidentata	0	11	4	22	0	0	0	0
*Ageratina adenophora***	13	16	4	0	0	0	0	0
*Pteris excelsa**	0	0	4	22	17	0	0	0
Sphaerocionium obtusum	13	21	0	0	0	0	0	0
Asplenium acuminatum	0	0	13	11	0	0	0	0
*Commelina diffusa***	0	16	4	0	0	0	0	0
Coniogramme pilosa	0	0	13	11	0	0	0	0
Marattia douglasii	0	0	17	0	0	0	0	0
*Nephrolepis multiflora***	38	5	0	0	0	0	0	0
Cyanea kunthiana	0	0	13	0	0	0	0	0
Digitaria sp.**	0	16	0	0	0	0	0	0
Elaphoglossum pellucidum	0	16	0	0	0	0	0	0
*Huperzia serratum**	0	11	4	0	0	0	0	0
*Gahnia gahniiformis**	0	0	0	0	0	13	8	0
*Paspalum urvillei***	13	11	0	0	0	0	0	0
Scaevola chamissoniana	0	16	0	0	0	0	0	0
*Cerastium fontanum triviale***	0	0	0	0	0	6	8	0
Clermontia kakeana	0	11	0	0	0	0	0	0
*Dactylis glomerata***	0	0	0	0	0	13	0	0
Dryopteris fusco-atra	0	0	9	0	0	0	0	0
Dubautia reticulata	0	0	0	0	17	0	0	0
Fragaria chiloensis sandwicensis	0	0	0	0	8	6	0	0
*Lythrum maritimum**	0	0	0	0	17	0	0	0
*Melaleuca quinquenervia***	25	0	0	0	0	0	0	0
*Ophioglossum pendulum**	13	5	0	0	0	0	0	0
*Pinus radiata***	0	0	0	0	0	13	0	0
Pittosporum glabrum	0	5	4	0	0	0	0	0

PLANT COMMUNITY CODE NUMBER OF RELEVÉS	A1 8	A2 19	B1 23	B2 9	B3 12	C1a 16	C1b 13	C2 11
*Plantago lanceolata***	0	0	0	0	0	6	8	0
*Psidium guajava***	13	5	0	0	0	0	0	0
*Pteris cretica**	0	0	0	0	17	0	0	0
*Setaria gracilis***	13	5	0	0	0	0	0	0
Silene struthioloides	0	0	0	0	0	0	15	0
Agrostis sandwicensis	0	0	0	0	0	0	8	0
*Asplenium fragile**	0	0	0	11	0	0	0	0
Carex sp.**	0	5	0	0	0	0	0	0
Clermontia grandiflora grandiflora	0	0	4	0	0	0	0	0
Ctenitis latifrons	0	0	0	11	0	0	0	0
*Cuphea carthagenensis***	13	0	0	0	0	0	0	0
Cyanea sp.	0	0	4	0	0	0	0	0
*Kyllinga brevifolia***	13	0	0	0	0	0	0	0
*Dryopteris insularis**	0	0	4	0	0	0	0	0
Dryopteris hawaiiensis	0	0	0	11	0	0	0	0
*Conyza bonariensis***	0	0	0	0	0	0	0	9
Eucalyptus sp.**	13	0	0	0	0	0	0	0
*Juncus effusus***	0	5	0	0	0	0	0	0
*Ludwigia octovalvis***	13	0	0	0	0	0	0	0
*Paspalum scrobiculatum***	13	0	0	0	0	0	0	0
Peperomia cookiana	0	0	4	0	0	0	0	0
Perrottetia sandwicensis	0	5	0	0	0	0	0	0
*Phymatosorus scolopendria***	0	5	0	0	0	0	0	0
Pittosporum confertiflorum	0	0	0	0	8	0	0	0
Pritchardia arecina	0	5	0	0	0	0	0	0
Rubus macraei	0	0	0	0	8	0	0	0
Sadleria squarrosa	0	0	4	0	0	0	0	0
*Trifolium repens***	0	0	0	0	0	6	0	0
Unidentified	0	5	0	0	0	0	0	0
Unidentified	0	0	0	0	0	0	8	0